THE MEANING AND PRACTICAL APPLICATION OF THE SPECIES CONCEPT

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Abstract

A brief outline is given of the processes used in ascertaining the limits of species in nature, and of the theoretical background on this subject. An explanation is given of the phenomena known as hybrids, races, and subspecies.

Introduction

The aim of this article is to provide some guidance to the naturalist who lacks special training in zoological systematics but who is interested in undertaking original work in this field, possibly with a view to publishing some results. Some zoologists advise against such persons making contributions to zoological literature. The fact remains that such contributions are made and are often useful.

I have omitted an explanation of elementary genetics even though I consider it basic to an understanding of the species concept, and hope that the reader will seek this information elsewhere. Similarly I have omitted discussion of the process of speciation which is dealt with at length but not exhaustively by Mayr (1963), and Dobzhansky (1951). The works of Mayr, Linsley, and Usinger (1953), and Mayr (1969) are exceedingly useful in preparing taxonomic work for publication. The rules for naming species are given in a publication by the International Commission on Zoological Nomenclature.

Development of the Species Concept

The concept of a species, though older than civilization, gained a more concrete meaning with the great number of descriptive studies and catalogues of animals and plants which appeared in the eighteenth and nineteenth centuries (and which still continue to appear).

To early workers the species was a "kind", a group of similar individuals having the ability always to reproduce their own kind, but above all having features in common which enabled their recognition as preserved specimens. To some more thoughtful zoologists organisms were considered to represent separate species if they could not be crossed to produce fertile offspring. Botanists, however, affirmed that their plant species could often be successfully crossed. Zoologists were slower to realise that some animal species could also be crossed with one another successfully.

The development of the science of genetics—the study of heredity—gave a deeper insight into the nature of species, and clarified aspects of the laws of evolution previously set forth by Darwin. The work of Dobzhansky and others focussed on species as natural populations of a certain kind, rather than odd collections of specimens typified by ma in zoos or museums. The most acceptable current view of the mea of species has been called the biological species concept becaus depends on the qualities of living individuals and populations. T definition of Mayr is here given as probably the most useful and gener acceptable.

Species are groups of actually or potentially interbreeding na populations which are reproductively isolated from one another.

The three principal aspects of this definition to be remembered a (1) A species consists of one or more natural populations of animals plants); (2) there is a continuity of interbreeding potential within throughout a species; (3) a species is unable to merge permanently populations of other species by interbreeding. "Reproductively isola means, as used in this definition, prevented from interbreeding by intr genetic differences. The definition only applies to organisms which produce by cross fertilization. It has no application to entirely s fertilizing organisms or those which always reproduce asexually. Spe limits in these organisms must be determined somewhat arbitrarily discontinuities of variation, preferably associated with ecological differe or geographical barriers.

Races

A species usually consists of few or many partly distinguish populations, which occupy different but not necessarily separated g graphic areas. Just as no two individuals are exactly alike, so no populations are identical. They always differ slightly or markedly in attributes of their individuals or in the proportions of individuals w different kinds of attributes. In general, populations which may be tinguished from one another by any degree of difference between attributes of their individuals are called races or geographic races.

Hybrids

Hybrids are the offspring of mixed matings between different spe or different races, or the descendants of such hybrid offspring. In animal kingdom hybrids between distinct species are generally v rare in nature, though hybrids between races may crop up almost whe different races of the one species come in contact. There are sev reasons why hybrids between related species are rare. Any two popula living together and producing indefinite numbers of fertile, viable hyb will tend to merge and lose their identity. Such populations will not be recognizable as distinct species. Often two species, even tho closely similar, are intersterile, that is cross-mating results in no offsp because of some incompatibility in the genetic systems or reproduc phyiology of the two species. Alternatively, the mixture of gene hybrid offspring may cause them to die before maturity or to be ste These factors do not altogether account for the extreme rarity (vir absence) of hybrids between many pairs of related species living toge under natural conditions, for we know that in some such cases fe hybrids can easily be produced by confining a mixed pair togethe captivity. In cases such as this it is clear that "mixed marriages" hardly ever occur under natural conditions, because the individuals simply refuse to mate with anything but their own species. However, in the artificial conditions of captivity, the normal behaviour pattern in disturbed and crossmating can take place. This has been proved for certain pairs of closely related species in birds, fish, butterflies, flies, and other animals.

There are some known cases where hybrids between populations can occur in numbers under natural conditions. An example is seen in the butterflies of the genus *Limenitis* in North America. Where the species *L. arthemis* and *L. astyanax* live together, fertile hybrids appear repeatedly, yet they do not cause the species populations to merge or lose their identity. A strong mating preference restricts the production of hybrids in the first place. But, as the hybrids are intermediates they might be expected to mate at least with one another, and it would appear that even a very slow rate of hybrid production from the pure strains should eventually swamp the differences between the populations by accumulating large numbers of individuals with every possible intermediate condition. That this does not happen is due to the inferior fitness of the hybrids relative to the pure strains. They simply cannot compete in the "struggle for existence" and are slowly but surely eliminated without making any permanent contribution to the population. This example illustrates a very important principle: each species in nature has a very highly co-adapted system of genes, evolved by natural selection, which results in a complex organism highly adapted to a mode of life peculiar to its species. Hybrids, particularly those between species, have lost this quality of co-ordination in their mixed gene systems and are less perfectly adapted to survive. This explains why there is such a general tendency among animals of all kinds to avoid mating with other species. Those which are not highly selective in choosing a mate waste their reproductive potential in producing hybrids which, even if viable and fertile, do not leave a permanent line of descendants. Consequently those remaining in the population are predominantly those which have inherited their parents superior ability to select an appropriate mate.

We should not too readily assume that an individual showing a combination of characters of 2 different species is a hybrid. There are some other possible reasons for apparent intermediates which cannot be considered here.

Use of Data

In practice we can apply the species definition to most animals and decide on the limits of species only when we can obtain enough information about them. We can look at two previously unknown butterflies and quickly summing up our impressions, we may say, "Those two are the same," or "Those two are different species." Our judgement may or may not be a skilful one, but it cannot be emphasised sufficiently that this approach does not constitute an adequate analysis of information in scientific research. Scientific Method is the basis of all good research, in Zoology, as in Physics and Astronomy. This method consists of recording data (pieces of information) directly from observation or experiment, intelligently examining the data as a whole to see if any particular inference

(hypothesis) can be drawn from it. The hypothesis only becomes wor
of permanent record (e.g. publication) when it has been adequa
tested against substantial data. When it can be affirmed that the hypoth
is the only one in conformity with the data, or much the most prob
one that fits the data, it becomes a useful theory. The theory must
carefully set forth with due consideration of the limits of its applica
and the meanings (definitions) of the terms employed.

The kind of data most generally available to us in systematics
the attributes or qualities of individual specimens known as charac
and the combinations in which these characters occur. Taxonomic ch
acters, i.e. characters that can be used in a systematic classification,
of many kinds. In general the easiest characters to use are morpholog
ones, including characters of coloration, form, and structure, in eit
the adult or immature stages. Sometimes these characters prove inadeq
for distinguishing reproductively isolated populations. We may then h
to consider physiological characters, chemical characters (e.g the ki
of amino-acids in the body, or kinds of secretions), or behavio
characters such as nest-building, courtship patterns, song, seasonal
currence, habitat preference, oviposition-site preference, and feed
preference. Some of these seemingly very subtle characters are of
utmost importance because they appear to be the means by which
animals recognize each other as belonging to their own kind.

We must be clear, when testing a hypothesis relating to species lim
how the data relate to the species definition. When our data consist
of characters and their combinations in individuals, we are using th
data to deduce if there is continuity or discontinuity of variation.
then use this as a criterion to tells us if there is reproductive contin
or reproductive isolation between the populations from which the
dividuals were drawn. Although this kind of evidence is often
informative and may provide reasonably definite conclusions it is
indirect evidence. Most importantly we should be aware that our
are the properties of our sample and not necessarily those of
populations from which the sample is drawn. The larger the sample
more likely it is to conform to the properties of the population, un
it is a biased sample. Heavily biased samples do not give a good ov
picture of the whole population because they have been taken, delibera
or advertently, more from one section of the population than anot
Samples which are selected for the largest, brightest, freshest, or m
ornamented individuals, or which are taken in one locality only, are
ideal subjects for systematic research. The worst samples of all
probably those heavily studded with rare aberrations. On the other h
samples from which extremes of variation are deliberately excluded
unsatisfactory.

It is a good idea initially to study as many different kinds
characters as possible, but experience in the study of any one group
generally indicate that some of these are much more informative t
others. In a great many insect families the external genitalia of
male provide far more reliable characters for species association th
any other structures. Their study is therefore obligatory in most work
systematic entomology. In many groups of animals and plants the num

and structure of the chromosomes provides useful information about species limits. The comparative study of chromosomes involves advanced microscopic techniques not usually available to the amateur.

Geographic Distribution

The definition of a species given above provides good criteria for making decisions about the status of populations which are in contact with one another. But where more or less similar populations live in total isolation from one another so that no migration between them occurs even over a prolonged period of time, then we have no way of telling if they are reproductively isolated or not under natural conditions. It has already been noted that experiments designed to test cross-breeding ability in captivity often do not tell us much about the situation in nature, unless they demonstrate inability to produce fertile hybrids. Because we cannot read the future, it would be useless to speculate on what might happen in the future if a barrier to dispersal broke down and the populations were again in contact under natural conditions. Probably most taxonomists would agree that inability to hybridise successfully under optimum conditions would justify species separation of geographically isolated populations. But it must be recognized that this criterion lies outside the species definition because the concept of reproductive isolation canont exist where there is total geographic isolation.

At this point it should be remembered that the species has long been established as a practical unit to which we can refer actual animals. Even the theoretical definitions are only aids in guiding practical taxonomy. A useful practical criterion of species distinction is always genetic discontinuity. It is scarcely practical to designate every geographically isolated population as a species on the grounds that there are always genetic differences between populations. A more reasonable approach, is to regard every such population as a species if it differs consistently in its taxonomic characters from other such populations. If a consistent difference is exceedingly slight, difficulty may again arise. It is therefore advocated that totally isolated populations should be regarded as separate species only when they differ consistently in at least two taxonomic characters.

Subspecies

The term subspecies is used for two different concepts in Zoology. Firstly there is the concept of the intergrading subspecies which is not sharply differentiated from adjacent subspecies with which it regularly interbreeds. This is, of course, a geographic race as defined above. Secondly there is the geographically isolated subspecies which is not sufficiently differentiated to be considered a species in the eyes of the systematist. Most of the "subspecies" of *Ornithoptera priamus* (Linné) (Lepidoptera, Papilionidae) are examples of this latter type (Zeuner, 1943). It is noteworthy that many of these so-called subspecies conform to the definition of geographically isolated species given above.

Wilson and Brown (1953) have criticised the subspecies as subjective and arbitrary in its taxonomic application. Their impressive series of arguments against the continued taxonomic recognition of subspe include the following: (1) the type-form of a subspecies often me represents a certain level, chosen by chance, within a cline; (2) diffe taxonomic characters often show independent geographic variation wi a species; (3) subspecific characters may repeat themselves in diffe parts of the geographical range of a species; (4) it has not been poss for zoologists to agree upon a lower limit for subspecies differentiati (5) insular subspecies, the only really distinct entities included in t category, could often just as easily and justifiably be regarded as spe (6) the allowing of subspecific names as nomenclaturally co-ordi with specific names has tended to clutter literature with a vaste num of names, all of which must be carefully recorded in case any of th should prove to apply to "good" species; (7) the local population of species is just as easily and more accurately designated by naming locality after the specific name instead of using a trinomial.

It is sometimes argued that the reducing of many less stro differentiated, geographically isolated forms from the species to subspecies level has simplified classification because it has reduced number of species recognized. A counter to this is the argument the simplification at the speces level has been more than compen for at the subspecies level, as systematists usually feel compelled catalogue all recognizable named subspecies, either in print or on ca

It would seem that a subspecies is often described when an au is in doubt as to whether a sample represents a distinct species or However the concept cannot be perpetuated solely for such dou cases; the subspecies has never been defined as a provisional spe

It is concluded that in most cases it is difficult to justify the estab ment of formally named subspecies.

References

Dobzhansky, T., 1951. *Genetics and the origin of species.* Columbia Univ Press, New York. 3rd edition. 364 pp.

International Commission on Zoological Nomenclature, 1961. International of zoological nomenclature adopted by the XV International Co of Zoology. London. 176 pp.

Mayr, E., 1963. *Animal species and evolution.* Belknap Press, Cambridge, 797 pp.

——— 1969. *Principles of systematic zoology.* McGraw-Hill, New York. 428 pp.

Mayr, E., Linsley, E. G., and Usinger, R. L., 1953. *Methods and princip systematic zoology.* McGraw-Hill, New York. 328 pp.

Wilson, E. O., and Brown, W. L., 1953. The subspecies concept and its taxo application. *Syst. Zool.* 2: 97-111.

Zeuner, F. E., 1943. Studies in the systematics of *Troides* Hübner (Lepid Papilionidae) and its allies etc. *Trans. zool. Soc. Lond.* 25: 10 figs 1-115.